PRESENT PROBLEMS IN PLANT ECOLOGY [1]

III. Vegetation and Altitude

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In the study of the relation of plants to environment, there are few problems of greater interest than those presented by the vegetation of mountains. The general facts are somewhat familiar, and reference to them is here necessarily brief. Whatever the vegetation of the surrounding country, mountains are usually forested; the forest is often composed of several zones in which different kinds of trees successively predominate; higher up the forests finally cease and give place to grassland of perennial herbs and low shrubs—these are some of the more general facts of mountain vegetation. There is bound up with them not only strangeness and beauty, but also a series of most interesting problems in the ecology of plants.

If I understand rightly the reason for this symposium, my duty is to state, as well as in brief compass I may, the present state of our knowledge in regard to these phenomena. In general, they rest back upon physical environment. In so saying, however, it must be kept in mind that biotic factors early modify the primitive physical ones; the reason for the occurrence or absence of a species may be the conditions created by other species.

The important factors which vary with altitude seem to be heat, light, precipitation, evaporation, and a factor made up of several of those named, namely, length of season. Let us consider these severally, and try how far

[1] A series of papers presented before the Botanical Society of America, at the Baltimore meeting, by invitation of the council.

we may at present determine the part played by each in connection with the plant life of mountains.

1. *Heat.*—From the days of Humboldt to the present, the vast importance of temperature in this connection has been recognized. In spite of this, our knowledge is rather scanty and vague. It has been usual to attribute great importance to the severe cold of mountain tops. This view, however, is entirely open to challenge. Mountains which rise up from warm plains certainly can not be invaded by plants which are killed by frost, but is there warrant in any physiological knowledge we now possess for supposing that extreme low temperatures are of any especial significance for plants which endure freezing? There is reason for believing that some woody plants are cracked by severe cold, but I believe the general question must be answered in the negative. That treeless mountain tops are not so because of great cold is shown by two facts: First, in cases that have been investigated, timber lines do not bear any direct relation to isothermal lines; and furthermore, forests do exist in the coldest districts on the globe. Herbaceous plants, too, taken even in the active condition, are known to survive extremely low temperatures, undisturbed.

We may note in passing the obvious fact that, for most low growing mountain plants, deeply buried as they are under snow, extreme winter temperatures do not come in for consideration at all.

That the lower temperatures of air and soil during the growing season are factors of great importance is not to be doubted. More specific information is not easy to obtain. Direct observation avails nothing, for we can hardly point to a single feature of anatomy or histology which is called forth by or conditioned upon heat or cold. In order to make further progress, recourse is naturally had to instrumental study. In the use of this method, many pitfalls await the worker. It is relatively easy to secure data of temperature, but *vastly difficult to interpret them.* It seems to me that, seeing a good

many ecologists are making use of temperature data, this point will bear some emphasis. Feeling that ecology is new, and exact instrumental work is the kind that counts, it is very easy, when one has secured a fine series of readings, or better still, a complete thermographic tracing for a growing season, to entertain the impression that he has accomplished something of note; whereas the fact in the matter simply is that if he has done his work well, it is of a quality with the routine work of a weather bureau. To relate the physical data to the manifold activities of a living plant is another matter, and calls for all the power of critical thought and all the knowledge of physiology which any man can command.

For our purpose, it seems possible to do little more than to point out some difficulties to be surmounted. To begin with, any method which assigns increasing values to higher temperatures must go astray as soon as the plant's optimum is passed, and for most of the plants we are dealing with, we do not know where that is. If, also, as there is some reason to believe, the growth-temperature curve has more than one maximum, a still further difficulty would be brought in.

Furthermore the ecologic optimum is made up of many harmonic optima, and may vary in different life phases of the same plant. In experiments in forcing fruit trees, it has been found that the optimum for blooming is markedly lower than for other periods for the plant's activity. Finally the temperatures recorded are for the soil or air, whereas the ones wanted are those that prevail within the plant. Leaves and shoots are warmed by sunshine and cooled by the evaporation of water. In this way temperatures may be brought about which differ materially from those recorded by a thermometer alongside. In the case of an Alpine plant, sheltered in some sunny angle of rock, how widely the temperature within its leaves may differ from that shown by a thermometer near by, properly set up for air temperatures in shade!

On the positive side, there seems less to be said. It

can not be doubted that the plant life of mountains is in no small degree modified and controlled by temperature, but who can put his finger on definite facts and say "this temperate forest is on this mountain in the tropics because of temperature," or "this Alpine plant is a dwarf because of cold." Strongly as we may suspect such points, we must be cautious about including them within the realm of our positive knowledge.

The peculiarities of Alpine plants have been thought to be due, in part, to great daily variation in temperature; that owing to the greater clearness and rarity of the atmosphere, the plant is more exposed to heating by intense sunshine by day, and cooling by more rapid radiation at night. Since growth takes place particularly at night, it seems evident that marked night cooling would lead to reduced size. That this is actually true has been proven by placing growing plants each night in the ice chest. At present more light is chiefly needed as to what temperatures are really experienced by Alpine plants over night. Air temperatures, at any rate, are more equable at high altitudes. In connection with the work in the Selkirks during the past summer, two complete thermographic records were taken, one meter from the surface, same hillside and exposure, at altitudes of 800 m. and 1,700 m., respectively. The daily maxima recorded at the upper station were notably less than at the lower; the nightly minima only slightly so. (Freezing point was not recorded for many weeks.) Such data accord well with the general results of meteorologists. They refer of course only to air temperatures.

Briefly summarizing, we may say that our knowledge of the relation of heat to mountain vegetation is not great. The importance of extreme low temperatures has been much overestimated. The significance of moderate temperatures is not yet capable of exact interpretation. The hypothesis of night cooling as a cause of alpine dwarfing needs further physical facts as a basis.

2. *Precipitation.*—That mountains are islands of

greater precipitation and that the vegetation of mountains is largely dependent upon atmospheric water are ideas familiar to every one. Schimper has further suggested that light showers at high altitudes favor the development of grassland rather than forest. This idea, to be tenable, requires the further assumption that the soil in the grassland zone is deficient in water supply. This may be true for lower latitudes, but it scarcely seems admissible for northern mountains where the late melting snows leave the soil supplied with all the water it can hold.

In quite a different way, too, precipitation in the form of snow becomes a decisive factor for vegetation. In a paper read before this society, a year ago, I showed that the timber line of the Selkirks was due to the heavy snow beds at those altitudes. By a coincidence, Cowles showed elsewhere, at the same time, that in a number of places in North America snow beds and timber line were causally related.

3. Closely connected with the question of heat and precipitation is another factor of prime importance in some mountains, namely, *Length of Season.*

In respect to this factor at least two points of view are necessary. For trees and plants growing on wind-swept spots, length of season is a question of temperature. For the vast majority of low-growing plants, on the other hand, length of season is also a question of emergence from snow beds to air and sunshine.

Taking up, first, the question of forests, it has been said that the total heat available at high altitudes is not sufficient for the maturing of new wood, and more particularly, that the season is too short for the ripening of good seed. Both of these ideas must stand or fall simply upon evidence, and so far as I am aware, none of a reliable character has been brought forward. It may be remarked that seedling trees usually seem abundant enough at timber line. It would be of interest to gather seeds of balsams, etc., growing at timber line and learn

if they germinated properly. When one considers the fact that elevated forests are usually coniferous, Myake's studies on photosynthesis by evergreen trees during winter become of interest. One may well inquire if trees of this kind obtain in this way a distinct advantage over others at high altitudes.

Turning to the low growing plants, we find their problems of a somewhat different nature. In the Alps, the Caucasus, the northern Rockies and the Selkirks to mention only a few examples, large tracts of lofty grassland lie buried under snow until the close of the vernal period. If one visits the higher forests of the Selkirks in June, he must journey in the snow. Arriving at the alpine fields, he finds them at the summer solstice, still hidden under an almost unbroken covering of white. In the month that follows, they will be gradually exposed. During the ten or fifteen weeks that remain, they must accomplish nearly the whole sum of their annual activities. The ability to do this must be a decisive factor in their struggle for existence. *Carex nigricans* ordinarily occurs mingled with other plants; but in moist hollows, where the snow has lingered until the middle of July, it often forms patches to the entire exclusion of competitors. Where the snow does not melt till the first of August, it is absent and the visible vegetation consists of polytrichum only. Where snow persists till late in August, the soil thus exposed is destitute of visible vegetation. Walking in the verdant alpine fields at the end of August, one finds each unmelted patch of snow bordered by plant societies in the order mentioned. Do we not read in this that of phanerogamous plants present the sedge is best able to compress its life processes into a brief period; that the moss is able to live with even shorter time allowance, but that even the moss is unable to maintain itself under conditions of such brevity of season as are represented by twenty or thirty days at the close of summer? It is hardly to be doubted that many other less easily traced questions of association and occurrence are decided by length of season.

4. *Light.*—Since a certain proportion of light is absorbed during passage through the atmosphere and particularly by the layers next the earth's surface, it seems plain that light becomes more intense with increasing altitude. If so, its relation to vegetation is a matter of much interest.

Notwithstanding that the question has received considerable attention, our knowledge of it is still in a rather unsatisfactory condition as will appear from the following:

Bonnier, Schimper, Schroeter and indeed most of those who have written upon the subject, express the belief that the more intense light is a factor of importance in connection with Alpine vegetation. They give reasons indicating that a greater intensity exists, and noting the reduced leaves and shoots and prominent flowers of alpine plants, state that the former is the cause—in part at least—of the latter. The conclusion, however, has not been put to the test of discriminating experiment.

Any further discussion of the subject brings in a general consideration of light as an ecological factor. I trust a brief digression may be permissible.

Since light is a form of solar energy, efforts have naturally been made to compute its intensity from astronomical data. Attempts have been made in several quarters to calculate light intensity for any day and hour of sunshine for the year at a given latitude. They do not, however, seem to have been happy in escaping fundamental error. For, in making calculations from the sun's altitude, there is not one varying factor, but several which must be reckoned with: (1) The amount of radiant energy falling upon a horizontal surface varies with the sine of the sun's altitude. This law is perceived by every one. It has sometimes been neglected, in the thought apparently, that since leaves stand at all angles, it is unnecessary to reckon what a horizontal surface may receive. Yet the direct light available for the total vegetation of a hectare or any other area is func-

tioned upon the angle made with the sun's rays. The law of the sine may, therefore, not be neglected. (2) Within the atmosphere we have the phenomenon of diffuse light from the sky. At the earth's surface it becomes a factor of no small importance, very likely surpassing for vegetation in general that of the direct rays of the sun. It is, of course, derived from direct light, but for it the law of the sine is far from valid. In general, it is subject to less variation. It is probably affected by many factors not easily observed, presence of dust, vapor, etc., and its numerical computation borders on the impossible. A table showing light intensity for any given day or hour, might possibly, if all factors were taken into account, show the value of direct light, but it is open to question, if this is what the botanist chiefly wants to know. (3) The length of the path of a ray of light through the earth's atmosphere, and, therefore, the fraction of it which is absorbed, increases with decreasing elevation of the sun. Quite apart from diminution due to decreasing angle of incidence, the light wanes as the sun approaches the horizon. This fact is sometimes clearly seen; sometimes apparently overlooked. (4) Absorption in the lower, denser, dust, water-vapor and carbon dioxide bearing layers of the atmosphere is relatively far greater than in the upper and rarer ones. This last holds good, especially for the shorter rays. This third consideration comes to the foreground in a study of altitude and vegetation.

Here then are several varying factors; some of them difficult to calculate, and none of which may be neglected. Moreover, as will be shown below, there is reason for doubting whether any theoretical calculations are valid, even for clear days.

Wiesner has carried on extensive studies upon light and plants, extending over several decades. He offers data to prove that light, for a given time and place, with cloudless sky, can by no means be calculated from astronomical data. His readings taken in different parts of

the world show astonishing irregularities. In Buitenzorg, the light diminished rapidly between eleven and twelve o'clock under apparently clear sky. Similar data were recorded for Cairo, Egypt. The maximum intensity obtained anywhere in the world was not in the tropics, but in Yellowstone Park. Though some of his results seem rather incredible, it must be owned that his methods appear ample and critical—far beyond anything else undertaken by a botanist. He has emphasized the distinction between direct and diffuse light. He finds the proportion of the former to increase greatly with altitude, and sees in this a factor of much importance for vegetation. His results in regards to altitude and light are not so full as could be wished, but he attributes the maximum observed in the Yellowstone to altitude, and, in general, assigns a high importance to light as a factor in alpine climate.

On the other hand, Clements states that in Colorado the variation of light with altitude amounts to a very small percentage and concludes that such differences as exist are too small to receive serious consideration in a study of mountain vegetation. The chief thing, therefore, that appears certain is that the whole question is in an unsatisfactory condition. In such a situation, one or two points must be kept clearly in view.

First, data as to light intensity must be obtained by methods which will pass muster with physicists. A certain body of such data are available. Time is lacking to take up the question here, but the work of Cayley, Violle, Langley and others might be cited to show that a considerable increase in light intensity with altitude does exist.

In the second place, it must be borne in mind that the relation of the plant to light is a complex one. In some of the work above quoted there seems to be the wholesale error of assuming that the importance of light for the plant is to be judged by observation upon its relation to the process of photosynthesis. It seems super-

fluous to emphasize that light is not only a source of energy, but a factor which now stimulates, now inhibits various activities of the plant in a profound degree.

It is the highly refrangible rays which suffer greatest absorption by the atmosphere. The light at the surface would, therefore, differ in *quality* from that at higher altitudes. In studying the question, it appeared to me desirable to learn whether any responses by plants could be found to alterations in quality—alterations, nevertheless, in which all kinds of rays should still be present. I therefore endeavored to set up experiments which should merely add a proportion of certain rays to an already sufficient daylight illumination. The results, while far from being as full and conclusive as could be wished, seem to indicate pretty clearly that plants do respond to such a variation in quality. Internodes were observably shorter and leaves more hairy under the bluer light.

Perhaps the whole question can be summed up in saying that the relation of vegetation to variations in light due to altitude are poorly understood; that more data from trained physicists would be welcome, but that the experiments still remain to be made which would enable us to interpret such data with confidence.

5. *Evaporation.*—Since pressure becomes less, wind velocity increases, and insolation becomes greater with increasing altitude, it has seemed necessary to conclude that the evaporation rate increases. Toward the summits of many mountains, *e. g.*, the White Mountains and Adirondacks, the decisive relation of wind to forest vegetation can hardly be doubted. In these cases there is good ground for assigning evaporation as the cause of timber line with all that it involves. The death of buds and twigs is probably chiefly due to drying in cold weather.

Most of the leading writers agree without question that evaporation is more rapid at higher altitudes. Schimper lays much emphasis upon it; Schroeter writes vividly of the drying of skin experienced by alpinists

and mentions the dry cured meat prepared by peasants in some places in the Alps, which, it is stated, is due to the greater drying power of the air. The reasoning is all but conclusive. There can be no doubt though, that the verdict of the soundest reasoning ought to be confirmed in the court of experimental evidence.

In 1907, Livingstone measured evaporation in the Santo Catalina mountains and found a *decrease* with altitude. This, perhaps, was not surprising, seeing that the series began in the desert below and extended to the cool mountain regions above.

During the past summer, I set up two series of instruments in the Selkirks at altitudes ranging from 800 m. to 2,900 m. Mountain flanks having a fairly uniform exposure were chosen, only short horizontal distances were involved, two stations were chosen at each altitude so that one might check the other. The season was favorable, being unusually warm and dry; one series was in perfect operation for twelve weeks. The results on the whole seem to exclude the idea that in the Selkirks evaporation increases with altitude. The maximum in each case was at the next lowest station, altitude of 1,100 meters. Above that there was a gradual and irregular diminution. It may be that the lower temperatures of higher altitudes more than offset the factors which make for increased evaporation. Indeed, it appears certain from the above data that for the Selkirks, such is the case.

The data in question, however, present only weekly totals. The possibility that excessive evaporation may take place during certain portions of the day, still remains to be studied. It must be ever kept in view, too, that it is not the absolute amount of transpiration which is so much of importance to the plant, as the balance between water supply and water loss. If the lower soil temperatures of higher altitudes make the obtaining of water more difficult, then the same or even a diminished evaporation rate might demand increased power of resistance on the part of the plant.

In trying to unravel the problems of mountain vegetation, it must never be forgotten that the plants of the present are descended from preexisting ones; facts of heredity are everywhere; phenomena that are found today not seldom hark back to conditions of the past.

In concluding, allow me to offer a plea for a service, which I have been thinking for several years would be one of the most helpful which could be rendered to this adolescent science of ecology, namely, that some one whose knowledge of physics and physiology fits him for such a task should overhaul and scrutinize our ideas and methods. Not counting minor and ephemeral papers, there can be no question that ecology, at the present time, contains not a little of discernible error. Rumors have been heard that zoologists are beginning to study ecology and looking to botanical methods for hints for developing their own. Within the family, it may be said that if wide-awake guests are coming, it is time to set the house in order. Moreover, ecology is finding a large place in elementary text-books, and in this way errors are being propagated. The interest alike of science and education in this field could in no way be better served than by a relentless pruning.

DISCUSSION OF PROFESSOR SHAW'S PAPER.

DR. LIVINGSTON: A remark was made by Professor Shaw in the beginning of his paper, which suggests that we sometimes lose sight of physical facts. A certain plant is not killed or shut out by the fact that other plants are near it, but by the fact that light conditions or moisture conditions or evaporation conditions or temperature conditions are different from those in which they might live. It seems to me that to speak of biotic and physical conditions leads to confusion; the thing the plant feels must be a physical thing.

PROFESSOR SHAW: In my remark I meant to clear up certain cases where one might lose sight of the fact that plants had largely modified physical conditions. I presume the very case which gave rise to that sentence was this: there are some reasons for supposing that in the Selkirks, the zone of greatest moistness, where lichens and mosses flourish is at something like 4,000 feet in altitude. A forest has developed there, and the condition of low evaporation rate has come about on account of that forest.